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Evaluating conservation and fisheries management strategies by linking spatial prioritization software and ecosystem and fisheries modelling tools

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Summary

1. Well-designed marine protected area (MPA) networks can deliver a range of ecological, economic and social benefits, and so a great deal of research has focused on developing spatial conservation prioritization tools to help identify important areas.

2. However, whilst these software tools are designed to identify MPA networks that both represent biodiversity and minimize impacts on stakeholders, they do not consider complex ecological processes. Thus, it is difficult to determine the impacts that proposed MPAs could have on marine ecosystem health, fisheries and fisheries sustainability.

3. Using the eastern English Channel as a case study, this paper explores an approach to address these issues by identifying a series of MPA networks using the Marxan and Marxan with Zones conservation planning software and linking them with a spatially explicit ecosystem model developed in Ecopath with Ecosim. We then use these to investigate potential trade-offs associated with adopting different MPA management strategies.

4. Limited-take MPAs, which restrict the use of some fishing gears, could have positive benefits for conservation and fisheries in the eastern English Channel, even though they generally receive far less attention in research on MPA network design.

5. Our findings, however, also clearly indicate that no-take MPAs should form an integral component of proposed MPA networks in the eastern English Channel, as they not only result in substantial increases in ecosystem biomass, fisheries catches and the biomass of commercially valuable target species, but are fundamental to maintaining the sustainability of the fisheries.

6. *Synthesis and applications*. Using the existing software tools Marxan with Zones and Ecopath with Ecosim in combination provides a powerful policy-screening approach. This could help inform marine spatial planning by identifying potential conflicts and by designing new regulations that better balance conservation objectives and stakeholder interests. In addition, it highlights that appropriate combinations of no-take and limited-take marine protected areas might be the most effective when making trade-offs between long-term ecological benefits and short-term political acceptability.

Key-words: Ecopath with Ecosim, Ecospace, marine spatial zoning, marine trophic index, Marxan, Marxan with Zones, systematic conservation planning

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Introduction

Marine ecosystems are under pressure, and in the rush to safeguard our oceans, conservationists are pinning their hopes on marine protected areas (MPAs). More than 7,000 MPAs have been established, covering 3% of global ocean area, with the aim of meeting a diverse set of conservation, social and economic objectives, including the management of marine resources (Watson *et al.* 2014). There is a growing consensus that by restricting certain activities within their boundaries, MPAs can provide numerous benefits for biodiversity and fisheries (Lester & Halpern 2008; McCook *et al.* 2010; Bates *et al.* 2013). Nonetheless, MPAs remain controversial and often face strong opposition from resource users who oppose restrictions on where and how they operate (Abbott & Haynie 2012; Rassweiler, Costello & Siegel 2012).

There is often conflict between conservationists and fisheries groups over the types of MPAs proposed (Grantham *et al.* 2013). For example, despite the socio-economic impacts associated with excluding all activities, no-take MPAs are generally preferred by conservationists because they offer better protection for marine ecosystems, and are easier to manage and enforce (Lester & Halpern 2008; Ban *et al.* 2011; Edgar *et al.* 2014). However, research has shown that partially protected MPAs, which are designed to restrict certain activities, can also provide a range of benefits, such as increased biomass, density and individual size of both target and non-target species, and species of conservation concern (Lester & Halpern 2008; McCook *et al.* 2010). Modelling studies have also shown that measures such as reducing fishing effort can be more effective at achieving conservation objectives, either alone or in combination with MPAs (Zeller & Reinert 2004). Thus, there are inherent trade-offs when choosing between types of MPAs, as no-take MPAs are seen as better for conservation but are often more contentious, making the process of implementation more politically difficult and polarizing (Le Quesne *et al.* 2008; Lester & Halpern 2008).

In this context, it is recognized that planners should seek to reduce conflicts when identifying the location and type of MPAs by accounting for social and socio-economic factors, as well as measures of conservation value (Grantham *et al.* 2013; Klein *et al.* 2013). Therefore, a commonly used approach to designing MPA networks is systematic conservation planning, a target-based approach to help identify priority areas that adequately represent species and habitats whilst minimizing impacts on fisheries and other sectors (Klein *et al.* 2013). This generally involves using spatial prioritization software tools, such as Marxan, which has been developed to identify priority areas efficiently (Ball, Possingham & Watts 2009). A recent extension of this software, Marxan with Zones, now enables so-called spatial marine zoning by allowing different management and protection zones to be explicitly considered in the analysis, together with their associated socio-economic costs (Watts *et al.* 2009; Klein *et al.* 2010).

However, whilst these software tools result in MPA network designs that minimize impacts on stakeholders, they do not consider the impacts of the different types of management proposed by policy makers. This is because they do not explicitly account for ecological processes and dynamics, and so it is difficult to determine the impacts these networks could have on marine ecosystem health and fisheries, or the implications for fisheries sustainability (Grantham *et al.* 2013). For example, closures and/or gear restrictions may induce shifts in the distribution of fishing effort and the targeting behaviour of fisheries, with potential cascading effects (Abbott & Haynie 2012). Fortunately, the last decade has seen the development of ecosystem models that can be used to address this problem; so here, we demonstrate an approach to explore the potential impacts of MPA management strategies by combining spatial prioritization software outputs with an ecosystem model.

To illustrate, we apply this method to the eastern English Channel, a region important for commercial fisheries, but also the focus of several on-going MPA initiatives (Metcalfe *et al.* 2013). This involved: (i) using Marxan and Marxan with Zones software to identify a range of MPA networks with different management types, based on zoning of fleet access and gear types; and (ii) using a spatially explicit ecosystem model developed in Ecospace derived from an Ecopath with Ecosim model (Christensen & Walters 2004) to investigate their ecological and fisheries impacts. More specifically, given the core problem in accounting for ecosystem dynamics in the planning of spatial management areas, we focus on how including different proportions of no-take MPAs relative to limited-take MPAs (i.e. partially protected) impacts ecosystem biomass, fisheries catches, commercially valuable species and the mean trophic level of landings. In doing so, we demonstrate a policy-screening approach that can help identify potential trade-offs between different management strategies, which is pertinent given global commitments to establish networks of effectively managed MPAs (Watson *et al.* 2014).

Materials and methods

MARINE PROTECTED AREA NETWORK DESIGN

We adopted a systematic conservation planning approach because it provides a transparent platform for exploring the role of management strategies in MPA network design (Grantham, Petersen & Possingham 2008). The analysis thus followed the principles of MPA network design by representing broad biodiversity surrogates (habitats) and species of conservation concern. This involved: (i) compiling biodiversity data on 34 species and 24 benthic habitat types in the eastern English Channel, known collectively as conservation features (see Table S1 in Supporting Information); (ii) setting representation targets for how much of each feature should be protected in UK and French waters; (iii) dividing the eastern English Channel into a number of $31{\cdot}4\ km^2$ planning units (Fig. S1) to match a system developed for an existing Ecospace model (Daskalov, Mackinson & Mulligan 2011); (iv) calculating the amount of each conservation feature in each planning unit; (v) assigning a cost to each planning unit based on vessel monitoring system (VMS) effort data for eight fishing fleets (beam trawls, demersal otter trawls, dredges, pelagic trawls, hooks and lines, nets, seines, and traps and pots); and (vi) using spatial prioritization software to identify a near-optimal set of planning units (referred to as portfolios hereafter) that when combined meet these representation targets, whilst minimizing fragmentation levels and planning unit costs (Ball, Possingham & Watts 2009; Watts *et al.* 2009).

We used both the Marxan and Marxan with Zones conservation planning software packages in our analysis. These have the same core functionality and use the same system for measuring costs based on the summed planning unit costs, a boundary cost that reflects the boundary length of the portfolio edge, and costs for not meeting the conservation feature targets. They both also use the simulated annealing approach, which involves running the software a number of times and identifying a series of different portfolios of planning units that meet specified targets whilst minimizing costs. Marxan, however, implicitly assumes that planning units can be assigned to one of two zones: reserved or not reserved. In contrast, Marxan with Zones is able to assign each planning unit to one of several user-defined management zones, allowing users to set targets for these different management zones and specify how costs vary for a particular planning unit depending on the zone to which it is assigned (Watts *et al.* 2009).

Given that Marxan and Marxan with Zones identify slightly different near-optimal portfolios each time they are run, we first needed to ensure that our investigation of the ecological impacts of MPA management scenarios was not masked by underlying spatial differences in the MPA networks. We did this by running Marxan 500 times and using the Cluster Analysis option in Zonae Cogito (Linke *et al.* 2011) to identify the five spatially most different portfolios (hereafter referred to as priority area maps) that met all the targets and minimized costs. These five priority area maps then formed the basis of our analysis, where we investigated the impacts of changing the percentage of each priority area map that belonged to two different management zones. These two zones were defined as: (i) 'no-take' that would exclude all fishing fleets and (ii) 'limited-take' that would exclude fleets using mobile bottom gears (beam trawls, demersal otter trawls, dredges), because these gears damage some habitat types and have been linked to stock declines (Roberts, Hawkins & Gell 2005). To do this, we used Marxan with Zones to modify each of the priority area maps and identify six portfolios based on setting targets that 0%, 20%, 40%, 60%, 80% and 100% of each conservation feature should be assigned to a limited-take MPA, with the rest being assigned to no-take MPAs. For example, the overall target for UK High Energy Infralittoral Rock was 3·6 km^2 (Table S1). Thus, in the first scenario, 3·6 km^2 (100%) was assigned to the no-take zone and 0 km^2 (0%) assigned to the limited-take zone; and in the second scenario, 2·88 km^2 (80%) was assigned to the no-take zone and 0·72 km^2 (20%) to the limited-take zone, and so forth. We set the cost of establishing no-take MPAs as being the combined cost of all eight fishing fleets (which were used as the planning unit costs in Marxan), whereas the cost for limited-take MPAs was based on fishing costs for the three excluded fleets using mobile bottom gears (see Appendix S1).

ECOSYSTEM MODEL

To describe the temporal and spatial dynamics of the eastern English Channel, we used Ecopath with Ecosim, a suite of modelling tools (comprised of Ecopath, Ecosim and Ecospace) that have been widely used to model marine food webs and analyse how changes might affect the structure and functioning of marine ecosystems (Christensen & Walters 2004). In this study, we used Ecospace, a policy evaluation tool based on spatially explicit simulation of ecosystem dynamics to investigate the impact of establishing MPA networks with different proportions of no-take and limited-take zones (Walters, Pauly & Christensen 1999). The spatial model was based on an existing (i) ecopath mass-balance model (Villanueva, Ernande & Mackinson 2009), which contained data on 51 functional groups (two marine mammal, one seabird, 29 fish, 15 invertebrate, two primary producers and two non-living groups to represent discard and detritus; Table S2) and eight fisheries (beam trawl, demersal otter trawl, dredges, pelagic trawl, hooks and lines, nets, seine, traps and pots, and a category 'other' to account for catches that could not be allocated to any of the above; Table S3), and (ii) Ecosim and Ecospace model (Daskalov, Mackinson & Mulligan 2011) that was derived from the Ecopath model and calibrated by comparing model outputs to time series (1973–2006) and spatial data from scientific surveys and fish stock assessments (see Appendix S2).

Ecospace simulations are structured around a base-map of cells to describe the two-dimensional spatial distribution of biomass for each functional group, and fishing effort over time (Walters, Pauly & Christensen 1999; Pauly, Christensen & Walters 2000). Movement between adjacent cells and the distribution of biomass are driven by parameters such as foraging behaviour, avoidance of predation and dispersal rates that are linked to specific habitat preferences (Walters, Pauly & Christensen 1999). This region is both physically and ecologically distinct from the adjacent western English Channel and North Sea, but not disconnected, and so application of the ecosystem model can be considered appropriate as the flow of energy within the boundaries is greater than those across (Vaz, Carpentier & Coppin 2007; Martin *et al.* 2009). Habitats and functional groups were thus assigned to each cell according to Vaz, Carpentier & Coppin (2007) who differentiated between four biotic communities in the eastern English Channel (Table S4). Dispersal rates for each functional group (Table S5) were determined from an existing North Sea Ecospace model which were based on published movement rates, and adjusted during Ecosim model calibration (Mackinson & Daskalov 2007; Daskalov, Mackinson & Mulligan 2011). For those functional groups with insufficient information, feeding and predation risk parameters that determine the relative dispersal, vulnerability and feeding rates in habitats to which they were not assigned were set to their default values, as per the existing Ecospace model (Table S5).

In addition, recognizing that fishing effort dynamics are important to consider when evaluating MPAs (Stelzenmüller *et al.* 2008), we specified steaming costs for each fleet based on the location of ports, where costs were calculated for each cell as relative distances to these ports (Daskalov, Mackinson & Mulligan 2011). We then defined the spatial distribution of the nine fishing fleets by assigning which habitats a fleet may operate in (Table S6) and used the gravity model in Ecospace to predict the spatial distribution of fishing effort, where the proportion of total effort allocated to each cell is assumed proportional to the relative profitability of fishing in that cell (Christensen & Walters 2004). These distribution maps were then visually inspected to ensure areas predicted as high effort in Ecospace reflected those which were high cost in Marxan. This is important, because if there are large discrepancies, one can assume that there are underlying issues with either the cost data used in Marxan or the distribution of fishing effort predicted by Ecospace that needs to be resolved to have confidence in the outputs derived from this process.

SIMULATING THE POTENTIAL IMPACT OF DIFFERENT MANAGEMENT STRATEGIES

To simulate the potential ecosystem responses to the different forms of management, we first ran Ecospace for 50 years until the distribution of biomass in the cells was equilibrated (i.e. the model was balanced prior to introducing management changes). We then overlaid each MPA portfolio onto the base-map and assigned which fleet could operate in each MPA according to their gear restrictions (Table S6), and ran Ecospace over a 50-year period (at 0·083 time intervals that are equal to monthly time steps). To examine how each management scenario affected ecosystem functioning and fisheries, we (i) compared the density of total and exploited ecosystem biomass and fisheries catches to baseline simulations of the eastern English Channel with no MPAs (i.e. fishing effort maintained at status quo); (ii) examined changes in the density of total and exploited ecosystem biomass inside and outside of MPAs at the end of the 50-year simulations relative to when MPAs were introduced (year 0); and (iii) investigated changes in the density of biomass inside and outside of MPAs for 13 functional groups (Adult Cod, Dab, Gurnards, Hake, Mackerel, Adult Plaice, Pollack, Adult Seabass, Seabream, Scad, Sole, Rays and Dogfish, and Adult Whiting; Table S2) of importance to commercial fisheries in the eastern English Channel (Martin *et al.* 2009). To reflect the exploited part of the system, we included only higher trophic level and commercially valuable functional groups, with a trophic level $\geq$2·35 (n = 29). This cut-off value was determined *post hoc* as 43% of the ecosystem biomass occurs below this trophic level due to the high abundance of benthic invertebrates and molluscs in the eastern English Channel (Table S2).

Finally, to evaluate the implications for fisheries sustainability, we used the 'Marine Trophic Index' (MTI). Whilst this indicator is often contested (Essington, Beaudreau & Wiedenmann 2006), it is currently endorsed by the Convention on Biological Diversity and is increasingly used to report changes in the health and stability of a marine ecosystem or area (CBD 2004). The MTI is a measure of the mean trophic level of fisheries catches; thus, a decrease in the MTI represents a decline in the abundance and diversity of higher trophic level species, highlighting that stocks are being overexploited and fisheries are not being managed sustainably as the trophic level of exploited species decreases (Pauly & Watson 2005). We calculated the MTI for the total fisheries catch for each year y as follows:

$$\mathrm{TL}_y = \frac{\sum_i (\mathrm{TL}_i * Y_{iy})}{\sum_i Y_{iy}}$$

where TLi is the trophic level for functional group i as estimated by Ecopath (Table S2) and Yiy is the catch of the functional group i in year y as provided by Ecospace. In addition, based on recommendations that this should be calculated to emphasize changes in higher trophic level and commercially valuable species that are often at a greater risk of overexploitation (Pauly & Watson 2005; Araujo *et al.* 2008), we also calculated the MTI to reflect changes in the exploited part of the system (trophic level $\geq$2·35; n = 29).

Results

ECOSYSTEM BIOMASS

The Ecospace model revealed that each of the proposed MPA management scenarios (Fig. 1) resulted in an increase in the density of total and exploited ecosystem biomass compared to a system with no MPAs (baseline scenario), particularly for MPA networks comprised of a large proportion of no-take zones (Fig. 2a, b). However, the change in total ecosystem biomass was typically smaller (Fig. 2a) than the change in exploited ecosystem biomass across each MPA management scenario (Fig. 2b). For example, after 50 years, a MPA network comprised of 100% limited-take zones increased the mean density of total and exploited ecosystem biomass by 0·19% and 3·41% relative to the baseline scenario. In contrast, a 100% no-take MPA network increased the mean density of total and exploited ecosystem biomass by 0·85% and 14·01%.

Additionally, each of the proposed MPA management scenarios resulted in an increase in the density of total and exploited ecosystem biomass inside no-take and limited-take zones (Fig. 2c, d). The change in ecosystem biomass, however, was greater for MPA networks that were comprised of a large proportion of no-take zones (Fig. 2c, d). For example, after 50 years, a MPA network comprised of 100% limited-take zones increased the mean density of total and exploited ecosystem biomass inside of limited-take zones by 0·56% and 8·60%. In contrast, the implementation of a 100% no-take MPA network increased the mean density of total and exploited ecosystem biomass inside of no-take zones by 2·27% and 39·30%. However, even though the change in density of total ecosystem biomass remained relatively constant outside of MPAs, increasing by approximately 0·5% across all MPA management scenarios (Fig. 2c), the density of exploited ecosystem biomass (trophic level $\geq$2·35) outside of MPAs decreased by approximately 5% (Fig. 2d).

FISHERIES CATCHES

The Ecospace model showed that each of the proposed MPA management scenarios also had a similarly positive impact on fisheries catches in the eastern English Channel, resulting in an increase in the density of total and exploited catches (Fig. 3a, b). For example, after 50 years, a MPA network comprised of 100% limited-take zones increased the mean total and exploited catch by 0·27% and 2·07% relative to the baseline scenario. In contrast, a 100% no-take MPA network increased the mean total and exploited catch by 34·5% and 39·5%, respectively. There was, however, an initial decrease in fisheries catches following MPA establishment (Fig. 3a, b). Whilst this decrease was greater for MPA networks that had a large proportion of no-take zones, catches typically took longer to return to baseline levels for MPA networks comprised

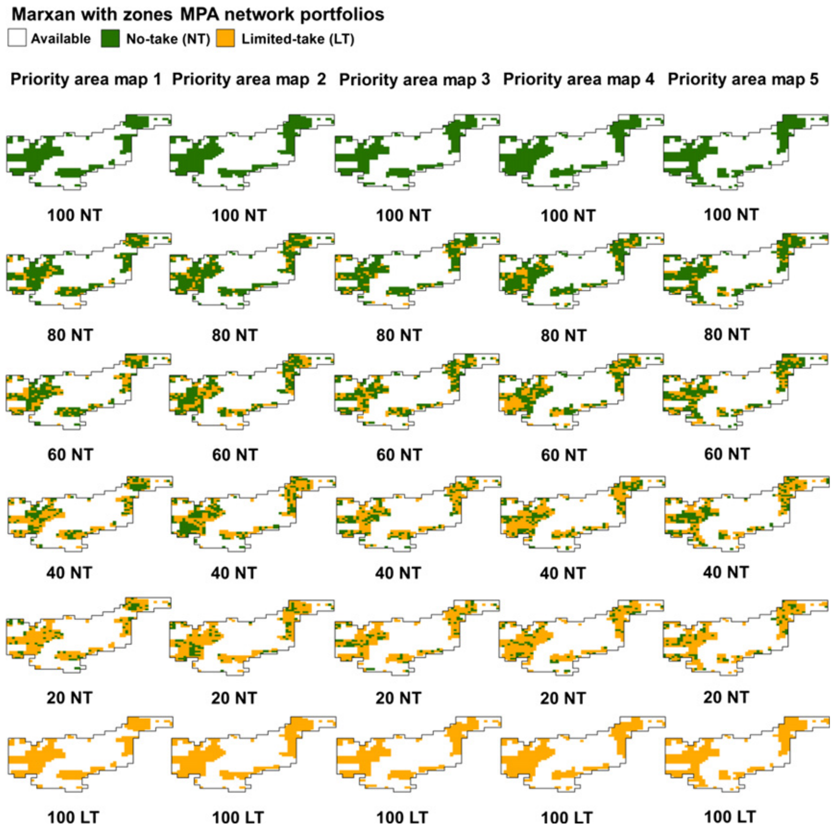

Fig. 1. Spatial configuration of the six MPA network portfolios produced using Marxan with Zones for each of five priority area maps identified by Marxan, where an increasing proportion of the targeted amount of each conservation feature is allocated to the limited-take zone.

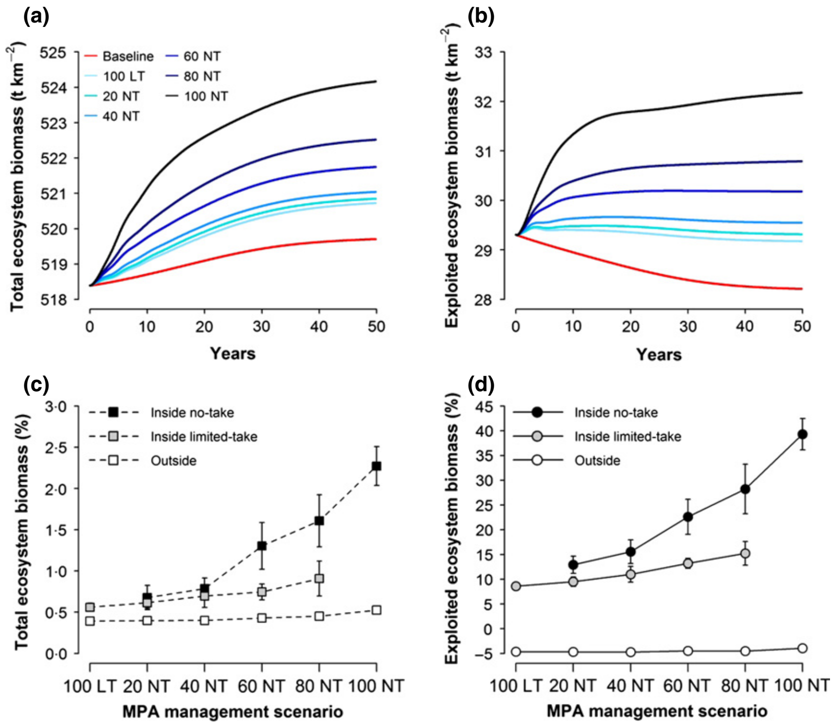

Fig. 2. Change over time (0–50 years) in mean (a) total and (b) exploited ecosystem biomass (t km^{-2}) relative to the baseline scenario with no MPAs (solid red line), and mean percentage change (±95% confidence intervals) in the density of (c) total and (d) exploited ecosystem biomass inside and outside of MPAs for each management scenario at the end of the 50 year simulations relative to when the MPA was introduced (year 0). Management scenarios defined as baseline (no MPAs), and MPA network portfolios comprised of 100% no-take: 100 NT; 80% no-take: 80 NT; 60% no-take: 60 NT; 40% no-take: 40 NT; 20% no-take: 20 NT; and 100% limited-take zones: 100 LT.

of a large proportion of limited-take zones (Fig. 3a, b). For example, total and exploited catches took 37·4 and 18·9 years, respectively, to return to baseline levels for a MPA network comprised of 100% limited-take zones, whereas total and exploited catches took 3·7 and 3·4 years to return to baseline levels for a 100% no-take MPA network. However, not all fisheries' fleets benefitted from MPA establishment; this was particularly evident for fleets

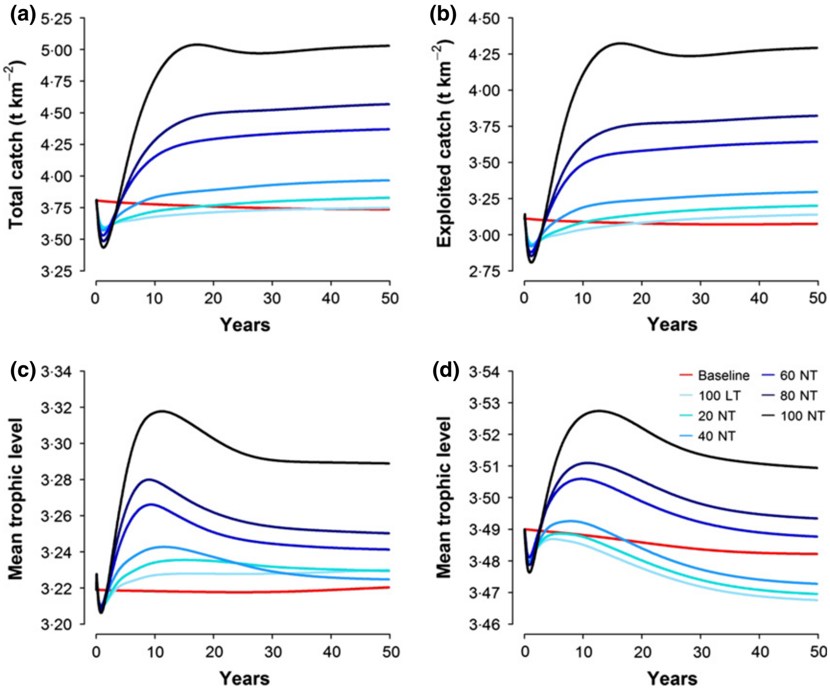

Fig. 3. Change over time (0–50 years) in mean (a) total and (b) exploited fisheries catches (t km^{-2}); and mean trophic level of (c) total and (d) exploited catches for each MPA management scenario relative to the baseline scenario with no MPAs (solid red line).

using mobile bottom gears (i.e. trawls and dredges), which generally experienced a small decline in fisheries catches across all MPA management scenarios as a result of being excluded from operating in both no-take and limited-take zones (Fig. S2).

COMMERCIALLY VALUABLE SPECIES

In the context of multispecies environments, the Ecospace model showed there are winners and losers associated with the different MPA management strategies, with some functional groups benefiting more from protection than others (Table S7). In terms of target species, the density of biomass for the 13 functional groups of particular value to commercial fisheries increased inside both no-take and limited-take zones across all the proposed management scenarios (Table 1). However, this increase was generally greater for MPA networks dominated by no-take MPAs, highlighting that the exclusion of all gears from MPAs is likely to result in substantially larger increases in the biomass of target species than the exclusion of mobile bottom gears only (i.e. trawls and dredges). For example, for MPA networks comprised of 100% limited-take zones, there was on average a 104%, 50% and 1046% increase in biomass inside MPA boundaries for sole, seabass and plaice, whereas a 100% no-take MPA increased the biomass of these species by 171%, 227% and 2483%, respectively.

MEAN TROPHIC LEVEL OF CATCHES

Under baseline simulations with no MPAs, the mean trophic level of total catches after 50 years was 3·22 (Fig. 3c), and the mean trophic level of exploited catches was 3·48 (Fig. 3d). The Ecospace model highlighted that each of the proposed MPA management scenarios had a positive impact on both the mean trophic level of total catches, which increased across all MPA management scenarios (Fig. 3c), and the mean trophic level of exploited catches (higher trophic level and commercially valuable functional groups), which were generally quite resistant to changes in management (Fig. 3d). There was, however, a very small decrease (<0·3%) in the mean trophic level of exploited catches relative to the baseline (i.e. fishing effort maintained at status quo) for MPA networks dominated by limited-take zones (Fig. 3d). For example, after 50 years, the mean trophic level of exploited catches for a 100% limited-take zone MPA network was 3·47; whereas the mean trophic level of exploited catches for a 100% no-take MPA network was 3·51.

Discussion

SPATIAL MARINE ZONING

Designing MPA networks that balance conservation and industry objectives has moved to the forefront of conservation planning. A key aspect of this involves working with relevant stakeholders and implementing agencies to develop a better understanding of the opportunities and costs associated with each type of conservation intervention (Klein *et al.* 2010). This is why spatial marine zoning has captured the interest of conservation practitioners as a means to protect biodiversity and manage fisheries, as it can spatially separate incompatible human activities and reduce conflict among user groups (Crowder *et al.* 2006).

Table 1. Mean percentage change in density of biomass (t km^{-2}) inside and outside of MPAs for 13 functional groups of importance to commercial fisheries at the end of the 50-year simulations relative to when the MPA was introduced, for each MPA management scenario (dark grey shading indicates an increase in biomass)

Functional group	100 NT Inside NT	100 NT Outside	80 NT Inside NT	80 NT Inside LT	80 NT Outside	60 NT Inside NT	60 NT Inside LT	60 NT Outside	40 NT Inside NT	40 NT Inside LT	40 NT Outside	20 NT Inside NT	20 NT Inside LT	20 NT Outside	100 LT Inside LT	100 LT Outside
Adult cod	51.38	−7.83	44.27	38.52	−8.12	39.32	36.22	−8.27	33.89	33.70	−8.40	31.71	31.67	−8.51	30.14	−8.54
Dab	4.36	−9.33	6.40	4.87	−8.78	7.90	6.25	−8.40	7.52	7.72	−8.03	8.23	7.73	−7.89	7.83	−7.81
Gurnards	30.67	−19.21	30.86	31.69	−19.43	31.85	30.09	−19.51	28.26	33.37	−19.52	36.26	30.78	−19.49	31.93	−19.59
Hake	39.84	3.59	34.87	36.05	3.35	34.99	26.86	3.44	26.57	31.48	3.37	16.97	30.96	3.47	27.87	3.64
Mackerel	58.97	−3.75	60.71	57.60	−3.41	64.18	55.41	−3.22	53.88	65.27	−2.95	52.79	62.40	−2.84	60.96	−2.72
Adult plaice	2483.06	24.75	2024.68	1581.94	16.89	1864.40	1300.88	10.78	1486.40	1226.47	6.04	1457.81	1100.92	2.66	1045.54	0.23
Pollack	14.36	−4.03	14.15	8.33	−3.79	14.51	8.62	−3.58	11.37	12.57	−3.49	7.45	12.39	−3.38	11.64	−3.23
Adult seabass	226.79	−5.41	117.21	76.83	−7.00	79.42	64.75	−7.63	66.73	57.62	−8.03	55.74	53.44	−8.17	50.39	−8.30
Seabream	9.12	−2.36	9.02	8.07	−2.44	8.78	8.38	−2.38	7.96	8.58	−2.33	8.73	8.25	−2.27	8.28	−2.19
Scad	8.45	0.34	7.25	5.97	0.18	6.72	4.48	0.36	4.62	3.05	0.26	2.88	2.04	0.19	1.24	0.30
Adult sole	171.16	1.06	144.30	127.27	−1.65	136.52	110.16	−2.62	112.25	116.05	−3.80	101.02	108.83	−4.25	103.51	−4.42
Rays and dogfish	35.33	0.07	28.38	28.17	−0.62	25.31	21.89	−0.96	19.75	20.76	−1.31	21.50	18.38	−1.30	18.03	−1.27
Adult whiting	109.10	−11.74	93.54	79.95	−13.65	88.10	71.90	−14.22	71.43	80.76	−14.31	72.41	77.79	−14.01	77.00	−13.76

In addition, research has shown that spatial marine zoning can also result in a reduced short-term socio-economic impact on fisheries, a more equitable impact on different fishing sectors, and a considerable increase in profits (Klein *et al.* 2010; Rassweiler, Costello & Siegel 2012). However, even with spatial marine zoning, there are almost inevitably trade-offs between conservation and fisheries objectives, regardless of whether systematic conservation planning has been used to help minimize these socio-economic impacts (Klein *et al.* 2008). Thus, if these trade-offs are not made transparent during the planning process, then we may not adequately conserve marine biodiversity or foster sufficient stakeholder support for conservation interventions (Klein *et al.* 2010).

Faced with these issues, it is important that policy makers assess the value of various management strategies, especially if they want to understand whether the benefits of no-take MPAs justify the costs of their implementation or whether others forms of spatial management could achieve similar results (Rassweiler, Costello & Siegel 2012). More importantly, stakeholders increasingly want to know how rapidly changes will occur after protection, even if natural variability can be difficult to predict (Babcock *et al.* 2010). Therefore, our approach that links widely used software tools could be used for policy screening to address these types of questions and so inform future management decisions by identifying trade-offs prior to implementation.

For example, in this study, we show that broader classes of MPA management based on zoning of fleet access and gear types not only reduce impacts on stakeholders in the eastern English Channel (Fig. S3), echoing the findings of similar studies (Klein *et al.* 2010), but could also provide conservation and fisheries benefits. This is important given that no-take MPAs are increasingly unpopular with the fishing sector in this region (Jones 2009). In particular, zoning of fleet access and gear types could represent a more politically feasible management strategy when compared to no-take MPAs that effectively exclude all access. Thus, in cases where zoning could result in long-term increases in target species biomass and fisheries yields as well as maintaining the sustainability of the fisheries, this information could help develop new regulations with broader stakeholder support (Rassweiler, Costello & Siegel 2012). In addition, excluding mobile bottom gears (i.e. trawls and dredges) from MPAs is likely to have positive conservation outcomes, leading to the restoration of habitat complexity and structure (Roberts, Hawkins & Gell 2005). This study, however, also clearly indicates that no-take zones should form an integral component of proposed MPA networks in the eastern English Channel. This is because for a given level of fishing effort, the model indicates they not only result in substantial increases in total and exploited ecosystem biomass, fisheries catches and the biomass of commercially valuable species, but are fundamental to maintaining the sustainability of the fisheries. Moreover, beyond their value to fisheries, no-take MPAs also contribute to biodiversity conservation goals, as they are often characterized by improved ecosystem health and resilience. Thus, they can act as an insurance policy against management failures elsewhere (Roberts, Hawkins & Gell 2005; McCook *et al.* 2010).

Despite the overall positive impact of introducing spatial management restrictions, it should be noted that there was an initial decrease in fisheries catches following MPA establishment, with the greatest impact associated with MPA networks comprised of a large proportion of no-take zones. However, it is worth highlighting that increases in catches often took decades longer to return to baselines levels when reducing the number of no-take MPAs in a network to one dominated by limited-take MPAs. This is likely because MPA networks comprised of a large proportion of no-take zones effectively reduce the available area open to fisheries, in contrast to MPA networks dominated by limited-take zones. Consequently, larger quantities of biomass are likely to build up inside MPA networks dominated by no-take MPAs and so spill over and/or migrate into surrounding areas, thereby contributing to increased fisheries catches more quickly. These findings thus highlight an inherent trade-off associated with adopting less contentious management strategies that is likely to have important and long-term economic consequences for fishers.

LINKING SPATIAL PRIORITIZATION SOFTWARE AND ECOSYSTEM MODELS

This study is the first to link these two widely used tools, and so it is important to acknowledge their assumptions and potential limitations if they are to be used to inform policy. First, ecosystem models will only be as good as the data that are used to create them. In particular, there is often considerable uncertainty surrounding the baseline model inputs that are used in Ecopath with Ecosim (Araujo *et al.* 2008), especially when accounting for the complexity of the interactions between the various components (i.e. species and habitats) in an ecosystem (Plaganyi & Butterworth 2004). Secondly, ecosystem simulations show expected outcomes for an environment that is structured in the same way as when the simulations begin, and so they do not address temporal changes in species distributions and interactions that could occur over time as a result of climate change, as has already been demonstrated in this region (Genner *et al.* 2004). Thirdly, ecosystem models assume the system is closed and that all the energy is consumed from within the system. Thus, the model may not make accurate predictions if species are known to move outside of the modelled system (i.e. pelagic species). Consequently, the results of these models should be considered in qualitative rather than quantitative terms as an aid to discussions on determining the appropriate type of management (Araujo *et al.* 2008). Although, where there is uncertainty, this approach could be used to investigate particular scenarios in more detail, accounting for complexities in trophic dynamics, changes in species distributions and interactions, and variability in fishing effort to ensure that predictions are based on a range of scenarios. This is important as model comparisons can result in a greater understanding of the likely effects of perturbations and management changes in an ecosystem (Fulton & Smith 2004).

However, despite these limitations, linking these widely used tools has the potential to make an important contribution to global conservation and fisheries management efforts (ICES 2012). This is because they can predict or at least provide warnings about otherwise unknown, undesirable or counterintuitive responses to changes in management (Araujo *et al.* 2008; Dichmont *et al.* 2013). Moreover, MPAs are not just fishery management tools and so given that the success of MPAs in meeting conservation objectives depends on user compliance, a key benefit of this approach is that it can be used to screen differing policy objectives (e.g. reference areas, offsets, oil and gas protected areas) and MPA zoning regulations (e.g. no-take, limited-take, cultural sites and community fishing areas) proposed by a range of stakeholders. This would require: (i) identifying the different types of management options that fit within existing policy frameworks; (ii) using spatial prioritization software to identify a range of MPA networks that meet these objectives; and (iii) using ecosystem models to inform stakeholders of the potential ecological responses to different types of management options, rather than making the common assumption that the resultant MPA networks identified by these software tools would benefit biodiversity and fisheries.

Additionally, given that planning unit costs are known to influence the location of priority areas (Ban & Klein 2009), these tools should be combined to investigate how different cost data used in Marxan could impact fisheries outcomes. Whilst this is likely to be complicated by the diverse group of stakeholders who operate in this sector, this is important as global conservation targets based on area alone will not optimize protection of marine biodiversity (Edgar *et al.* 2014). More specifically, for MPA networks to be effective management tools, regulations need to be strategically designed to foster stakeholder support and ensure user compliance (McCook *et al.* 2010; Rassweiler, Costello & Siegel 2012; Edgar *et al.* 2014), and so future work linking these tools should consider a range of actors and costs in the planning process.

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Data accessibility

All Marxan, Marxan with Zones conservation planning software files and Ecospace model outputs have been deposited in the Dryad repository: doi:10.5061/dryad.h68bj. Ecopath, Ecosim and Ecospace models and supporting technical documentation on parameterization available on request from Cefas and Ifremer (Ecopath, Ecosim and Ecospace input data, composition of functional groups and model parameters uploaded as online supporting information) Metcalfe *et al.* (2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Marine protected area network design methodology.

Appendix S2. Description of eastern English Channel Ecosystem model inputs and parameters.

Appendix S3. Description of the marine protected area network portfolios produced using Marxan and Marxan with Zones.

Table S1. Details of the conservation features and targets used in the Marxan analysis.

Table S2. Ecopath input data and composition of the species included in each of the 51 functional groups.

Table S3. Economic data for the eastern English Channel fleets.

Table S4. Distribution of the functional groups as assigned to habitat types in the eastern English Channel.

Table S5. Relative dispersal rates, feeding and predation risk parameters of functional groups in Ecospace.

Table S6. Defining fisheries in Ecospace as assigned to habitat types and MPAs in the eastern English Channel.

Table S7. Change in density of biomass inside and outside of MPAs for each functional group at the end of the 50 year simulations.

Fig. S1. Eastern English Channel planning region.

Fig. S2. Change in catch per fisheries fleet for each MPA management scenario.

Fig. S3. Details of total area and cost for the MPA network portfolios identified by Marxan and Marxan with Zones.